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THE CAUSES OF VEGETATIVE CYCLES[1]

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1. The demonstration of vegetative cycles

The work of the past decade has shown most clearly that there are cycles of vegetation, which are comparable precisely to cycles of erosion; in each there is a period of youth, which is characterized by vigor of development and by rapidity of change; in each there is a period of maturity, and finally one of old age, which is characterized by slowness of transformation and by approach to stability, or at least to equilibrium. At the close of the vegetative cycle there is no such universal feature as the base level of the physiographer, since the final vegetative aspect varies with the climate, and hence is called a climatic formation. In the eastern United States, the final stage is a mesophytic deciduous forest; farther to the north and in the Pacific states, it is a coniferous forest; in the great belt from Texas to Saskatchewan, the final stage is a prairie; and in the arid southwest, it is a desert. In every case, the ultimate or climatic plant formation is the most mesophytic which the climate is able to support in the region taken as a whole. In a prairie climate there may be trees, but they occur for the most part near lakes or streams, or in protected depressions, and in the base-leveling of the region they give way to the prairie; quite the same may be said of trees in a desert climate.

It has been ascertained that the original plant formations in any habitat give way in a somewhat definite fashion to those that come

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after. Pioneer formations usually are hydrophytic or xerophytic, mostly xerophytic in arid climates, and more equally divided in moist climates. For example, the last retreat of the glacial ice left in our northern states a vast tract made up essentially of hills and hollows, the hollows, if deep enough, with lakes. The first vegetation of the hills was xerophytic, and the first vegetation of the hollows, hydrophytic. Finally, except on the higher hills and in the deeper hollows, these first plant formations gave way step by step to the climatic tundra, and, as the climate became ameliorated, this in turn gave way to climatic coniferous forests, and then to climatic deciduous forests as they exist today. So far have the higher hills and the deeper hollows lagged behind the less extreme habitats in their development that there are still to be found many places which continue to have pioneer formations, though, of course, they differ greatly from the original pioneer formations of the tundra.

While the general trend of vegetation is from diversity toward uniformity, it must not be supposed that complete similitude is ever reached even under like climatic conditions. There are species, for example, in the culminating forest of New England which do not occur in Ohio, and species in Ohio which do not occur in Illinois; southward the difference is even more pronounced. And yet it cannot be denied that from the Maritime Provinces to Minnesota and south to the coastal plain the ultimate forest in its larger features is of a single type; the percentages and even the kinds of dominating trees may differ, but the aspect is essentially the same. Much more diverse from one another than are the beginnings or the ends are the intervening stages. Our northern lakes, for example, differ much less from one another in their floristic composition than do the swamps to which they give rise. The initial stages of a rock upland in Tennessee and in northern Michigan are much alike, both in aspect and in floristic composition; the terminal stages in these two widely separated districts are even more alike, but the intermediate stages are very different, northern Michigan having nothing at all comparable to the oak stages in the vegetational development of eastern Tennessee, and the latter region being without the complex coniferous stages of northern Michigan.

In this instance it is likely that some of the northern coniferous stages correspond to some of the southern oak stages; thus we may speak of *alternative* or *substitute* stages, when different plant formations occupy equivalent places in a successional series.

In a desert climate an upland may exhibit almost no succession, since the original xerophytic formation may remain with but little change; in comparison with a successional series in a mesophytic climate, one may speak here of the *elimination* of certain stages. In marked contrast to the lack of succession or to the slow succession on a desert upland is the rapid succession on uplands in humid climates; indeed, it is possible here for mesophytes to exist side by side with xerophytes in the pioneer stages—in such a case one may speak of *telescoped* successions. Even in a climate like that of the eastern United States, telescoping may take place, as in the successions of rich fallow land and in those which follow the cutting of a mesophytic forest. With this brief survey of recent progress in the field of physiographic ecology, we may pass to a similarly brief consideration of the historical development of vegetative dynamics, and then to a consideration of the main theme of the address.

2. The development of dynamic plant geography

The systematic exploitation of developmental or dynamic plant geography presupposes the establishment of the principles of dynamic geology and of organic evolution; hence it could not have antedated LYELL, who brought general recognition of the former, or DARWIN, who brought general recognition of the latter. Results frequently lag far behind their causes, and it is only now, a full half-century after the publication of DARWIN'S *Origin of species*, and three-quarters of a century after the appearance of LYELL'S *Principles*, that the dynamic method is coming to be regarded as the most fundamental thing in plant geography. As in other branches of science, there have been prophets far in advance of their time, though it is only within the last decade that the prophetic insight of these pioneers has had recognition. LYELL records the struggle of the developmental idea in geology, as opposed to the ruling theories of special creation or catastrophism, noting especially the keen philosophy of certain ancient Greeks

and the renascence of these views in Italy through the influence of LEONARDO DA VINCI and of other great contemporaries and followers.

So far as we know, the beginnings of dynamic plant geography are much more recent than are the beginnings of dynamic geology, nor is this strange, since it is easier to recognize the destruction of land by waves and the deposition of material by rivers than to observe the more silent transformation of one plant association into another. Doubtless the earliest observers of such transformations failed to record the things they saw. It is hardly to be doubted, for example, that long ago many a philosophic woodsman must have noted, when he cut down the trees of a forest, that there sprang up a new vegetation differing from the old, and that gradually these first trees of the newly developing forest were displaced by other trees; and there may have been some who were keen enough to see that, after a long time, there was a return to the primeval type of forest.

The earliest account which I have discovered that clearly deals with vegetative dynamics is in a short paper in the *Philosophical transactions* in 1685, in which WILLIAM KING (**1**) gives a good account of the origin of bog vegetation from floating mats; many times since, this has been reported as an original discovery. Perhaps the first to have a real glimmer of the doctrine of succession, as understood today, was the great French naturalist BUFFON. Although better known for his splendid descriptions of animals, BUFFON in his earlier life was much interested in forestry, and in 1742 he noted (**2**) that poplars precede oaks and beeches in the natural development of a forest. As a result of this observation, he gave the important advice to foresters that if they wished to cultivate beeches, they should plant them not in the open, but in the shade of those trees which they naturally succeeded. BIBERG (**3**), a student of the great LINNAEUS, published his thesis in 1749, and in this he describes the gradual development of vegetation on bare rocks; here he observes accurately the pioneer activity of the lichens and mosses, and he notes as well the importance of *Sphagnum* in the development of bogs.

The seeds planted by BUFFON and BIBERG fell on sterile soil; in

France it was observed that BUFFON was trespassing on theological grounds, and he was obliged to recant any views which implied that the world was not made in the beginning once for all; in Sweden the influence of LINNAEUS was wholly against anything dynamic; he never published anything dynamic himself, and when a student like BIBERG set his face in that direction, the master frowned, and said that the student was departing from the true mission of the botanist. It is not strange, therefore, that there followed a sterile period of three-quarters of a century. Yet it was within this period that plant geography was first recognized as a definite branch of science, for this was the period of HUMBOLDT. This also was the period of JOACHIM SCHOUW, who published the first general plant geography, and of the older DECANDOLLE, who gave the weight of his great name to several important treatises in the new subject. But none of these men, not even HUMBOLDT, were permeated with the dynamic principle, so far at least as plant geography is concerned. They placed descriptive plant geography on a solid foundation, and gave it such momentum that for a full century it dominated the entire field of plant geography; indeed in certain places it dominates plant geography today.

France, so often the birthplace of great ideas, gave the pendulum an impulse in the right direction. The sane influence of BUFFON had not altogether been suppressed by the theologians, and finally there arose such men as JUSSIEU, who introduced a flexible natural system of plant classification, which finally displaced the rigid artificial system of LINNAEUS, thus making possible the development of evolutionary theories; such men as LAPLACE, who conceived a theory of planetary evolution, thus making possible the development of evolutionary theories in other lines of science; and such men as LAMARCK and GEOFFROY STE. HILAIRE, who propounded evolutionary theories in biology. The birth of dynamical conceptions in France a century ago rejuvenated science throughout Europe, making possible the development of a LYELL and a DARWIN. It also made possible the development of a dynamic trend in the new science of plant geography, though, as previously noted, the momentum given to descriptive geography was too great readily to be overcome.

Very properly the first work of the new period along dynamic lines was done in France; in 1825 DUREAU DE LA MALLE (**4**) published the first paper which gave the results of a careful study of plant succession involving the observations of a number of years. His work was done mainly in cut-over areas of forest, and no work done since greatly surpasses it in accuracy and thoroughness. The marvelous clear-sightedness of DUREAU DE LA MALLE is well shown in the title of his chief contribution, which (in English rendering) is: "Memoir on alternation or on alternative succession in the reproduction of plant species living in association (*société*)—is it a general law of nature?" DUREAU DE LA MALLE (not STEENSTRUP, as frequently supposed) first used the term succession in the present sense; probably he was the first also to use the term society as an expression of plant grouping. The year 1845 is a noteworthy one because it was then that EDWARD FORBES gave a short paper (**6**) before the British Association, opening up an entirely new line of study, namely, the interpretation of past geographic features by the present. He was the first to understand the significance of endemism in relation to previous connections between islands and continents that now are isolated.

In 1841 a great advance was made by the Danish geologist STEENSTRUP (**5**), who discovered the possibility of using the fossils of the immediate (i.e., postglacial) past as a means of interpreting the climatic changes and the correlated vegetation changes of recent epochs. VAUPELL, a student of STEENSTRUP, but more botanically inclined, applied his ideas in detail (**7, 9**), and in the years between 1851 and 1863 gave to the world his famous account of the postglacial development of Danish vegetation, showing that the birch was the chief early pioneer, and that later it was followed in turn by the pine and the oak, and finally by the beech, which dominates today. From 1856 to 1859 REISSEK (**8**) worked out the dynamical development of the vegetation on the islands of the Danube. In 1876 GREMBLICH (**10**) seemed to realize the actuality of cycles of vegetation. In 1881 HULT, a Finnish botanist, made the first comprehensive study of succession (**11**) as it is now taking place in a given region, and he was the first to recognize that a comparatively large number of pioneer plant associations later

give way to a comparatively small number of relatively permanent associations.

In 1888 TREUB, whose recent premature decease we so keenly regret, began the study of the new vegetation of Krakatoa (**12**), thus inaugurating one of the most fruitful lines of investigation in dynamic plant geography. In 1891 WARMING, to whom more than to any other we owe the present large place occupied by ecological plant geography, published the first of his developmental studies of Danish dune vegetation (**13**). This was followed by a similar treatment of the Rhône delta by FLAHAULT and COMBRES (**14**), and of the North German heath by GRAEBNER (**16**), and also by WARMING'S *Plantesamfund* (**15**), the original Danish edition of his well known *Plant geography*, in which there is much material of dynamic import, together with the formulation of a number of "laws of succession." In 1896 MEIGEN (**17**) made a systematic study of succession, somewhat along the lines previously followed by HULT, and he showed that there is a final tendency toward equilibrium. This brings us to the period in which dynamic plant geography was taken up actively in this country, and here our historical résumé may well give place to the main topic of this paper.

3. The delimitation of successional factors

No systematic attempt has been made hitherto to group in an analytic manner the phenomena of succession from the standpoint of their causation. WARMING (**15**) made a great advance toward this end by gathering together the known records of vegetative change or succession; he noted that vegetative change is particularly evident on new soil (as along sandy shores, and in marshes, on lava, on landslip soil and talus, and on burned and fallow land). He summarizes his studies by giving six laws appertaining to succession. CLEMENTS (**21**) attempted to distinguish between primary and secondary successions, the former being those on newly formed soils, and the latter those on denuded soils. This classification seems not to be of fundamental value, since it separates such closely related phenomena as those of erosion and deposition, and places together such unlike things as human agencies and the subsidence of land. CLEMENTS, like WARMING, gives a summary of results in the form of laws.

While most observers very properly have paid chief attention to the actual facts of succession rather than to their underlying causes, a scrutiny of past results shows very clearly that the phenomena considered have differed greatly in kind. Obviously the phenomena of bog development, as observed by WILLIAM KING, had to do with a succession in which the activities of the plants themselves played the leading part; the humus accretions of the bog plants, such as the peat moss *Sphagnum*, made possible the development of another vegetation on a higher soil level. In a comparable manner, the successions observed by BUFFON, by BIBERG, and by DUREAU DE LA MALLE had to do with plant activities; the forest trees of a given generation cast the shade necessary for the development of other trees which need shade rather than light for their development; BIBERG'S lichens accumulated a soil which made possible the development of higher vegetation on rock surfaces. STEENSTRUP, however, in his study of the fossils, introduced to the scientific world a new kind of succession phenomena, for in his elucidation of the postglacial history of Denmark there were recorded changes of broader significance than those hitherto observed; it was clear that the transition from the tundra vegetation through the birch and pine vegetation to the oak and beech, as developed by him and by his student VAUPELL, was a record of climatic change, inasmuch as the very same horizontal succession may be observed today in journeying from northern Scandinavia to Denmark. A third and equally diverse kind of succession phenomena was recorded by REISSEK in his study of the islands in the Danube, for here there was clearly recognized the influence of physiographic change on vegetation. Thus in succession we may distinguish the influence of physiographic and of biotic agencies. The physiographic agencies have two aspects, namely, regional (chiefly climatic) and topographic.

4. Regional successions

Regional successions are so slow in their development that they can be studied almost alone by the use of fossils. Hence the experimental method, which has proven so potent in unraveling many a biological tangle, is here of no avail. It is not strange, therefore,

that these successions are and probably must remain the least understood of all. There are, perhaps, four great examples of extensive regional change, which may be accepted as demonstrated, namely: (1) the change from the Carboniferous to the Permian, which is made evident particularly through the replacement of the carboniferous ferns, fern allies, and primitive gymnosperms by the *Glossopteris* flora and later by the modern gymnosperms; (2) the subordination of the gymnosperms to the angiosperms in the Cretaceous; (3) the elimination of tropical forms in boreal regions in the late Tertiary; and (4) the postglacial invasion of southern forms into boreal regions accompanying and following the retreat of the glacial ice. Generally it is held that the dominating factor in these vegetative successions is climatic change, and that this climatic change is chiefly one of temperature. Of this there can be no doubt in the case of the changes immediately before and after the Pleistocene ice invasion. The constant relation between glaciation and the development of the *Glossopteris* flora in the Permian makes it likely that the general vegetative changes of that epoch also were due primarily to temperature.

On the whole, however, there has been a general tendency to overestimate the influence of temperature as an ecological factor. The trend of nearly all experiment has been to show that water is of vastly greater importance, and it well may be that the change from the atmospheric humidity which seems to have characterized the Carboniferous to the aridity which seems to have characterized the Permian had more to do than did the decreased Permian temperatures with the elimination of the carboniferous flora and with its replacement by mesozoic forms. The most puzzling of the great vegetative transformations of the past was the sudden change from the dominantly gymnospermous forests of the Jurassic to the domination of the world by angiosperms in the Cretaceous. We know that after the Permian there was a gradual climatic amelioration toward genial conditions similar to those which characterized the Carboniferous; this amelioration seems to have culminated in the Cretaceous, which, like the Carboniferous, was also a period of extensive base-leveling. Very probably the high temperatures and the great atmospheric humidity of the Cretaceous gave con-

ditions that particularly favored the angiosperms, which as a group are much more mesophytic than are the gymnosperms.

To summarize on regional successions, it would seem that secular changes in climate, that is, changes which are too slow to be attested in a human lifetime, and which, perhaps, are too slow to be attested in a dozen or a hundred lifetimes, are the dominating factors. It is possible that these changes sometimes are more rapid than at other times, and there are those who would have us believe that the climate now is growing warmer, as witness the rapid recession of many of our North American glaciers; there are others who are quite as sure that the climate is growing colder, as witness the southward retreat of the "timber line" in Scandinavia. Still others feel equally confident that the recession of glaciers is due to increasing aridity; this explanation has the advantage also of accounting for retreating "timber lines." And there yet remain some who believe that all such changes may be of short duration, as it were cycles within cycles, or feeble and short-lived oscillations of great climatic waves. It is to be pointed out that great earth movements, either of elevation or subsidence, that is, the far-reaching and long-enduring epeirogenic movements, as contrasted with the oscillations of coast lines, must be considered in accounting for regional successions; the elevation of the Permian and the base-leveling of the Cretaceous must have played a stupendous part in instituting vegetative change.

5. Topographic successions

In striking contrast to secular successions, which move so slowly that we are in doubt even as to their present trend, are those successions which are associated with the topographic changes which result from the activities of such agents as running water, wind, ice, gravity, and vulcanism. In general these agencies occasion erosion and deposition, which necessarily must have a profound influence upon vegetation. I have considered in another place and in some detail (**18, 19, 20**) the influence of most of these agencies, and it will suffice in this place to summarize a few of the leading kinds of phenomena that are involved. As might be expected, the influence of erosion generally is destructive to vege-

tation, or at least retrogressive (i.e., tending to cause departure from the mesophytic), while the influence of deposition is constructive or progressive (i.e., tending to cause an approach toward the mesophytic). Progressive successions are well illustrated in the development of flood plains along rivers, and in the growth of sandy shores; retrogressive successions are associated with the eroding activities of streams and of receding shores.

Sometimes erosion may not have a retrogressive influence and sometimes the effect of deposition is not progressive. For example, on a somewhat rapidly eroding clay cliff of Lake Michigan, there often occur certain xerophytic annuals, which develop during the comparatively stable summer period, and a few perennials, such as the sumac and *Equisetum*, which have underground organs that enable them to migrate landward as fast as the cliff recedes; here we have a remarkable instance of rapid topographic change without a corresponding plant succession, either progressive or retrogressive. A marked increase in erosive intensity would destroy all vegetation, and a marked decrease in erosive intensity might institute a progressive vegetative succession. Deposition unaccompanied by progressive changes may be illustrated by an instance from the Lake Michigan sand dunes. Frequently a growing dune is inhabited by xerophytic annuals and by a few shrubs or trees (as various willows and the cottonwood); such a place illustrates the extreme of topographic dynamics, but often the vegetation is static. A great increase in depositional intensity results in the destruction of all the plants, while a decrease in depositional intensity results in progressive succession. Retrogression or a static condition of vegetation is to be seen also along rapid streams, where there is a considerable deposition of coarse material. A striking illustration of retrogression associated with deposition is afforded by lava flows.

6. Biotic successions

A. GENERAL FEATURES

Of less interest, perhaps, to the physiographer than are the vegetative changes hitherto considered, but of far greater import to the plant geographer, are the vegetative changes that are due to

plant and animal agencies. These are found to have an influence that is more diversified than is the case with the physiographic agencies; furthermore, their influence can be more exactly studied, since they are somewhat readily amenable to experimental control, but particularly because they operate with sufficient rapidity to be investigated with some exactness within the range of an ordinary lifetime. If, in their operation, regional agencies are matters of eons, and topographic agencies matters of centuries, biotic agencies may be expressed in terms of decades.

It has been seen that changes of climate or of topography generally institute vegetative changes; indeed this would have been predicted to be the case, even without examination. But at first thought it seems somewhat striking that far-reaching vegetative changes take place without any obvious climatic change and without any marked activity on the part of the ordinary erosive factors. Indeed, it is probably true that the character of the present vegetative covering of the earth is due far more to the influence of these relatively silent and subtle factors than to the more obvious factors previously considered. So rapid is the action of the biotic factors that not only the climate, but even the topography may be regarded as static over large areas for a considerable length of time. It has been said that many of our Pleistocene deposits exhibit almost the identical form which characterized them at the time of their deposition; in other words, the influence of thousands of years of weathering has been insufficient to cause them to lose their original appearance. These thousands of years would have sufficed for dozens and perhaps for hundreds of biotic vegetative cycles. Many a sand dune on the shores of Lake Michigan is clothed with the culminating mesophytic forest of the eastern United States, and yet the sand dunes are products of the present epoch; furthermore, sand is regarded generally as a poor type of soil in which to observe rapid succession. If a clay upland were denuded of its forest and its humus, it is believed that only a few centuries would suffice for the mesophytic forest to return.

From the standpoint of dynamic plant geography our land areas are divided into two well marked categories: on the one hand is the erosion topography that is characteristic of the eroding and

depositing phases of present streams and shores, and on the other hand is the *pre-erosion* topography (as it may be termed) which is characteristic of those areas that have not as yet been invaded by erosive forces. In our northern states the areas characterized by the presence of a pre-erosion topography often greatly exceed in extent the areas which are characterized by an erosion topography. South of the glaciated region, however, the areas characterized by the presence of an erosion topography often greatly dominate. But the influence of biotic agencies is not confined to areas that are characterized by a pre-erosion topography. For example, in our eastern forested region the development of a ravine, which furnishes a characteristic illustration of rapid topographic dynamics, exhibits only here and there actual erosion or deposition; the ravine slopes as a whole are covered with a mesophytic vegetation, because at a given spot the interval between periods of active erosion often is sufficiently long to permit the development of an entire biotic cycle. Perhaps in no other way could there be brought out more strikingly the durational contrast between topographic and vegetative cycles; a ravine is an index of extreme topographic youth, and yet in its development there is ample time for the complete development of many vegetative cycles. Quite as in ravines, the cliffs of streams and shores often exhibit temporary exemption from erosion, whereupon there is at once instituted a biotic cycle, which often has sufficient time for complete development before erosion again becomes active.

B. THE HUMUS COMPLEX

a. Water.—It is now time to consider the varying aspects of the biotic agencies which institute succession. Of these the first to be mentioned, because of its unquestioned supremacy, is the accumulation of humus. There are a number of different ways in which the accumulation of humus affects the trend of succession. It can scarcely be doubted that the most important of these humus influences, and perhaps the most important of all influences, inheres in the change which the humus brings about in the water relation of the soil. Speaking generally, humus accumulation occasions an increase in soil moisture on uplands and a decrease in

soil moisture in depressions; hence it is probable that the changed water relation due to humus accumulation is the dominating factor in determining the mesophytic trend, both in hydrophytic and in xerophytic habitats. Although bare sand supports a xerophytic flora, the accumulation of a thin humus layer is sufficient for forest development, and the Michigan dunes show that the most mesophytic of our forests can grow on a sand dune, if there is present a humus layer a few centimeters in thickness. On rock uplands, lichens commonly are the first humus accumulators; not only do they contribute humus by their own decay, but they give shelter and anchorage to plants of higher order, whose humus-accumulating capacity is greater. As long as the vegetation is open, and the humus exposed to the sun and wind, accumulation is slow, because of oxidation. But when the vegetation cover is more fully developed, the humus is more and more protected and hence accumulates more rapidly.

The relation of swamp successions to humus accumulation is particularly close. For each level both below and above the water table, there is a characteristic plant formation. In the deeper ponds only submersed aquatics can develop, but after a time their humus débris accumulates to such an extent that plants with long stems or leaf-stalks (such as the pondweeds and water lilies) are able to develop. They in turn build up the humus and prepare the way for their own elimination and for the development of such plants as the bulrush, which grows in shallow water. The latter again prepare the way by further humus accumulation for the first land plants, and they again for others. In all this well known successional series, the dominating factor clearly is a decreasing water content due to the accumulation of humus.

b. Soil organisms.—Another important influence associated with humus accumulation is the increase of soil organisms. These may play a part scarcely second to water, but as yet we know all too little of their activities to be certain of their precise place in the scale of importance. We know, however, that nitrogen is one of the essential plant constituents, and that it is made available chiefly by certain bacteria and fungi. Since these forms live on decaying organic matter, it seems likely that humus accumulation

is likely to favor their increasing development and hence an increasing supply of available nitrogen. A single instance will suffice to show the possible importance of soil organisms in succession. The beech, which is a characteristic member of the culminating forest of the eastern United States, has roots which are enveloped by saprophytic fungi; it is believed that these fungi represent the absorptive system of the tree, and it is likely also that they are able to make nitrogen available, since so many similar fungi are now known to possess this power. In any event, the beech is known to depend upon the fungus, being unable to flourish without it. Obviously, then, the beech cannot appear in a successional series until its associated saprophytic fungus finds conditions requisite for its development in the soil. It is likely, too, that other saprophytic organisms are detrimental to various green plants, thus becoming a factor in their elimination. There is opened up here a great field of investigation, and all that can be stated now with definiteness is that it is likely to be demonstrated that the accumulation of humus is of profound significance in the development of successive saprophytic organisms, and probably on this account in the succession of the higher plants.

c. Toxicity.—Still another humus factor that seems likely to be of large significance, but whose exploitation is so recent that we cannot yet appraise it, is soil toxicity. It has been known for a long time that the roots of plants give off various excretions, but it is only through the recent careful work of LIVINGSTON and his associates (**22**), and later of SCHREINER and REED (**25, 26**), that we have come to know much concerning their nature and influence. In the case of wheat it has been ascertained that the roots give off certain substances which are deleterious and perhaps actually toxic, especially to wheat. Such results should not occasion surprise, since it is well known that many bacteria excrete substances which retard or even prevent the further growth of their own kind.

One of the greatest puzzles to the student of plant dynamics has been afforded by the successional series in bogs, since in spite of the wet soil there are many plants that obviously are xerophytic. There is universal agreement that there is something in bog soils

which is detrimental to plant growth, but there have been various theories as to its nature. Some years ago LIVINGSTON (**23**) discovered that bog waters have an effect on the growth of algae which is quite comparable to the effect of various toxic agents. More recently DACHNOWSKI, following the lead suggested by SCHREINER and REED, has been making a careful study of bog toxins (**27, 28**). On account of the poor drainage of bogs, there is no other habitat where root excretions would be more likely to remain. Year by year these excreta would accumulate, thus making the bog more and more unfitted for the development of ordinary hydrophytes; hence for a time the dominating bog plants would be those which would be able to withstand the acids and other deleterious excreta given off by the roots or produced subsequently by changes in the accumulating humus. However, when these bog xerophytes bring the humus level well above the water table, the deleterious plant products will be more and more oxidized, and ultimately there will be produced a soil of such character that ordinary mesophytes may flourish in it. While there is much in this theory which still requires confirmation, it certainly accounts for most bog phenomena and is not controverted by any known facts. It is likely also that some of the accumulating soil compounds may be of importance in neutralizing deleterious inorganic or organic soil constituents. In any event, the study of soil toxins and of their varied relations to plants is one of the great fields of investigation for the future.

d. Food.—Perhaps there are some who would have supposed that the chief significance of humus accumulation lies in the increased amount of plant food that thus is made available. Once it was supposed that the well known luxuriance of plants in humus is due to the large amount of plant food which it contains. Long ago this luxuriance was shown to be in the main due to other causes, but recent experiments have demonstrated that ordinary green plants are able to absorb certain foods (as glucose), and it may be that such plants actually utilize in this way some of the substances of the humus. It is likely that the increasing food supply in accumulating humus is an important factor in the succession of the soil organisms, but as yet this subject has never been investigated.

It also offers a fascinating field for study. The depletion of mineral foodstuffs in the soil has been urged as a successional factor, but it is doubtful if this is of any consequence. The great abundance of the mineral constituents of plants in nearly all soils is in strong contrast to the minute amounts which the plants contain. Furthermore, the plants in their decay return to the soil the mineral elements which they took from it.

e. Temperature and aeration.—Finally humus accumulation alters the soil temperature and the air content of the soil. For the most part changes in air content and in temperature probably are insufficient to be of great influence in vegetative change. In bogs, however, there is evidence that each of these factors is of importance. TRANSEAU has shown (**24**) that in the growing season the temperature of the water and of the soil in bogs is below that of other soils, and of the superincumbent air. Such a condition certainly is detrimental to root activity. Similarly TRANSEAU (**24**) has shown that the lack of aeration in bog soils is detrimental to root activity. Thus for these reasons (and probably also because of soil toxicity, as noted above) certain stages in bogs are characterized by the development of a xerophytic vegetation, since the unfavorable conditions for root absorption make existence in bogs difficult for any plants with aerial organs except such as have structures which reduce transpiration. That such bog plants are actual and not merely apparent xerophytes was demonstrated in brilliant fashion by TRANSEAU (**24**), who produced plants with xerophytic structures from ordinary plants by growing them in bog conditions.

C. SHADE

Next in importance to humus among the dynamic biotic agencies is shade. The foresters have known for generations that in the reforesting of a region the first trees to appear are those which require a large amount of sunlight for their development; conspicuous among such light-requiring pioneers are the poplars and birches. Rarely is a dense growth of these trees followed by trees of similar kind, since the increasing shade makes the development of seedlings of these species more and more difficult. Other trees, however, perhaps pines and oaks, are able to thrive in a degree of

shade which aspens and birches might not be able to endure. Finally the pines and oaks in turn may be succeeded by such trees as the beech, the sugar maple, and the hemlock, since these trees are able to develop in a considerable amount of shade. The latter trees may continue indefinitely, unless climatic or topographic changes intervene, since, unlike most species of trees, their seedlings are able to develop in shade as dense as that which is cast by the parent trees. While the influence of increasing shade, as here set forth, is undoubted, the extent of its influence is not known; *pari passu* with the increase of shade, and partly on account of it, there goes on the accumulation of humus. On uplands in our climate each of these factors tends to bring about the development of a mesophytic forest, but as yet it is impossible to determine which has the more potent influence. Increasing shade favors the mesophytic trend of upland successions in yet another way than through its direct influence and through its effect upon humus accumulation; the cutting off of light results in increased atmospheric humidity and hence in decreased evaporation. Some recent observations by FULLER (**29**), as yet unpublished, show that the pioneer plant formations of the Indiana sand dunes are characterized by high evaporation, and that this evaporation progressively decreases until the minimum is reached in the climatic forest.

In contrast to ordinary uplands is the influence of light upon the development of vegetation in lakes. At the outset there are many lakes which are too deep to have a conspicuous vegetation of green plants on the bottom. Through the accumulation of inorganic detritus and of humus, the latter arising from the decay of green plants living in the upper waters and from the decay of other organisms at all levels, there gradually is made possible the development of a plant formation on the bottom, composed of plants which require only a miminum amount of light. In succeeding years the shallowing of the lake makes possible a greater and greater development of green herbage, unless the development of a rich floating vegetation again cuts off the light. It is obvious that the influence of light and shade on succession is not so explicitly related to life as is that of humus; humus can arise only from organisms, but shade may be cast by many other things than trees. The rapid develop-

ment of a mesophytic forest in a canyon is due in large part to the increasing shade which is cast by the walls as the canyon deepens. However, the predominating influence of shade certainly is in connection with forest development, and hence it is not unfair to group it with biotic influences.

D. PLANT INVASION

A further biotic influence is that of plant invasion. In the long period of geologic history, plant migrations from one region to another must have played a tremendous part in the changing aspect of vegetation. There is reason to believe, however, that such changes, apart from those due to human influence, have been wrought almost as slowly as those due to climatic change. So imperceptibly do these migrations take place that we know of no profound change that has been wrought by this means in natural floras within historic time.

E. MAN

The last of the biotic influences to be considered is that of man. Most of the factors hitherto considered, especially increasing shade and accumulating humus with its varied kinds of influence, cooperate to transform originally hydrophytic and xerophytic plant formations into those that are more mesophytic; that is, they institute progressive successions. The influence of man, however, almost without exception, is retrogressive. Human culture reaches its highest expression in mesophytic climates or on mesophytic soils; the xerophytic soils of rocky crags and of sand barrens are unfavorable places for human exploitation, and the desert is for man an unprofitable waste, except where he finds an oasis or makes a district mesophytic through irrigation. Similarly, the waters are of value chiefly as avenues of transportation and as a source of food, not as a habitation; and swampy tracts are considered valueless, unless made mesophytic by drainage. Man, therefore, in seeking a place of abode, in clearing land for agriculture, and in his search for timber, has destroyed chiefly mesophytic vegetation, in other words, the very vegetation which, in most areas occupied by human culture, has been seen to be the culminating plant formation.

When a forest is destroyed by cutting, the succeeding vegetation commonly is more xerophytic than that which was destroyed, because of increased light and decreased humus. The influence of fires is much more retrogressive, because the vegetation of the forest floor, as well as the trees, is destroyed, and also because the humus is more largely oxidized. Both in such areas as these which gradually return to the forest, and in other areas which are prevented from making such return, on account of their use for cultivation, or for habitation, or for grazing animals, there enter among the pioneers a large number of cosmopolitan weeds which follow in the train of man. Most of these weeds are of xerophytic tendencies, and hence are well fitted for these pioneer stages. In the revegetation of fallow land and in reforestation, these immigrants soon disappear, giving way before the returning native forms which inhabited the region before man entered with his destructive axe and torch.

F. PLANT PLASTICITY

Before concluding this section on biotic agencies, there should be noted some instances where dynamics in the habitat meets with a reaction other than that of succession. Very frequently in the draining of a pond by humus accumulation, the same plants may be found in different stages, but characterized by a change of aspect. For example, the mermaid weed (*Proserpinaca*), the water hemlock (*Sium*), and the water smartweed (*Polygonum amphibium*) are fitted for existence in a shallow pond and also in a swamp where the soil level is above the water table. In the former instance the plants possess so-called water leaves, which vary greatly in form and structure from the air leaves, which are seen in the following swamp stage. Such amphibious plants thus have the power through their great plasticity of existing in two distinct plant formations; many of their companions, however, in the two situations are quite unlike, indicating that the habitat range of the latter is narrower, on account of their smaller plasticity.

In the western forests, the Douglas spruce may be a xerophytic pioneer, and yet may remain through all the stages of forest development, including the culminating mesophytic forest; this remark-

able tree may even dominate in each of the stages. The Douglas spruce differs from the amphibious plants in that it exhibits no such striking changes in leaf habit in the different conditions in which it lives; however, the change in the accompanying vegetation is much more profound than in the swamp, for at the outset the Douglas spruce may be accompanied by xerophytic pines and junipers, and at the close by the mesophytic hemlock and by a luxuriant carpet of mesophytic ferns and mosses. Thus it is clear that the life range of some plants is very broad and of others very narrow; obviously the latter are the best markers of habitat dynamics, for with a change of conditions they soon give way to other forms. Of especial interest to the physiologist is the situation in such plants as the Douglas spruce, whose leaves without change of form or structure seem equally fitted for light or shade, for dryness or humidity.

7. Conclusion

It is not to be supposed that all the influences which are involved in plant succession have been outlined in the preceding pages. Indeed, some minor contributory factors have been purposely omitted, because of the brief time allotted upon such an occasion. However, it is to be hoped that the dominating factors, so far as known at present, are here mentioned. From a survey of the various agencies involved, it seems clear that the influences which bring about succession differ profoundly in their nature, and also in the rapidity of their action. Although they grade into one another as do all phenomena of nature, we may recognize climatic agencies, which institute vegetative cycles whose duration is so long that the stages in the succession are revealed only by a study of the record of the rocks. Within one climatic cycle there may be many cycles of erosion, each with its vegetative cycle. The trend of such a cycle can be seen by a study of erosive processes as they are taking place today, but the duration of the cycle is so long, that its stages can be understood only by a comparison of one district with another; by visiting the parts of a river from its source to its mouth, we can imagine what its history at a given point has been or is to be. Within a cycle of erosion there may be many vegetative cycles, and among these are some whose duration is so

short that exact study year by year at a given point makes it possible to determine not only the trend of succession, but the exact way in which it comes about. We can see one stage replacing another before our eyes, and hence we may hope some day, if we exercise sufficient ingenuity and patience, to understand the underlying causes of the change. It is clear therefore that vegetative cycles are not of equal value. Each climatic cycle has its vegetative cycle; each erosive cycle within the climatic cycle in turn has its vegetative cycle; and biotic factors institute other cycles, quite independently of climatic or topographic change. It is small wonder that within this complex of cycle within cycle, each moving independently of the others and at times in different directions, dynamic plant geography has accomplished so little in unraveling the mysteries of succession. It may be some small contribution to this end, if the preceding considerations assist in delimiting the problems.

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